ORIGINAL RESEARCH

Needle in a Haystack: Predicting the Occurrence of Wetland Invertebrates on the Basis of Simple Geographical Data. A Case Study on Two Threatened Micro-Mollusc Species (Gastropoda: Vertiginidae) from Poland

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Abstract The aim of this study was to evaluate whether simple geographical data can be used to predict the probability of the presence of two threatened snail species: *Vertigo angustior* and *V. moulinsiana,* occurring within wetland areas across their central European range. Our research was based on data from 226 localities across Poland fitting with the species requirements according to the current literature. We used Canonical Variance Analysis with variance partitioning and tree classifications to model relationships between the species presence/absence and rough geographic features describing each locality (landscape and geomorphological types and hydrography). Our results have shown that the localities of the studied species are related to particular types of landform and landscape and are not distributed uniformly. Both species occur predominantly in young postglacial lowland landscapes and are usually associated with particular succession stages of lakes, with *V. moulinsiana* occurring in earlier phases of habitat evolution. Results from modelling show that cost- and time effectiveness of surveying for these species could be substantially increased by avoiding particular location types. The prediction models presented will be a useful tool for planning future surveys of the vertiginids and in studies on their ecology and distribution.

Introduction

Studies on small invertebrate species are often challenging since such species are easy to overlook. The problem is even more pronounced when the target species are rare and/or protected—conservation plans tend to be based on incomplete distribution data. Many countries try to effectively protect such species simply by protection of their habitats (e.g. Natura 2000 network in Europe, Endangered Species Protection Program and U.S. Fish and Wildlife Services in USA, National Conservation Plan in Canada). Not all of these habitats however will host the species and—on the other hand—not all of the localities hosting such species had been discovered and/or taken under the conservation schemes. The problem and, thus, reduction in extinction risk of isolated populations require a reliable methodology for surveys of such localities (Egoh et al. 2014).

Such methodology should include a testable and easy-to-use prediction framework, enabling selection of the most promising sites for fieldwork and omitting those in which probability of finding the species is negligible (Guisan et al. 2006). The development of such a methodology will increase the time- and cost effectiveness of the surveys. It will also enable foreseeing potential conflicts of interest between nature conservation and industry on the level of investment planning. Such a method of prediction should be adjusted to the ecology

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of particular species and should be based on results of a number of surveys covering a wide geographical range. It is especially needed for species that are difficult to detect in the field, because in such cases the gains from reducing the study effort will be greatest.

One of the most endangered invertebrate groups are the molluscs. They have the highest number of documented extinctions of any major taxonomic group, with non-marine species constituting 99 % of all molluscan extinctions (Lydeard et al. 2004). Snails are often one of the most suitable groups when assessing the state of endangered habitats (Bedford and Godwin 2003; Ponder and Walker 2003; Steinitz et al. 2005; Stewart 2006; Ormerod et al. 2010; Murugesan et al. 2011; Oke 2013). Some *Vertigo* species, for instance, constitute an important element of well-preserved fen habitats (e.g. Šefferová Stanová et al. 2008) and are used as one of the indicators of wetland integrity in the European Union under the Habitats Directive (Colling and Schröder 2005a, b). Additionally, the role of terrestrial molluscs in litter decomposition and nutrient cycling in ecosystems is substantial (Cook 2001; Bardgett 2005). Thus, detecting the most endangered molluscan species and implementing conservation measures may also assist in the preservation of endangered ecosystems (Ormerod et al. 2010).

The main goal of our research was to find a way to make the surveys for potential wetland sites of endangered gastropod species more effective. We used simple geographical data to check if such information can be useful when predicting which areas have the highest and lowest probabilities of the presence of two snail species: *Vertigo angustior* (Jeffreys, 1830) and *V. moulinsiana* (Dupuy, 1849) within their central European range. Both snails are threatened across the EU and listed in Annex II of the UE Habitats Directive and in red lists of many European countries (Książkiewicz 2014). Their small size (the height of the shell does not exceed 5 mm) and cryptic way of life (they are often litter- or soil-dwellers) make studies of these species complicated and time-consuming (Horsàk 2003).

In central Europe, *V. moulinsiana* and *V. angustior* are known to occur in open wetland localities where moisture levels are high and relatively constant (e.g. fens and sedge meadows, Pokryszko 1990; Killeen 2003; Książkiewicz 2010). However, *V. moulinsiana* is more restrictive with respect to moisture level than *V. angustior* and usually inhabits permanently wet or temporarily flooded areas (Killeen 2003; Cameron et al. 2003). *V. moulinsiana* prefers habitats that are overgrown with tall monocotyledons, moving up and down the stems to obtain desired humidities (Pokryszko 1990; Hornung et al. 2003; Killeen 2003; Myzyk 2011; von Proschwitz 2003). In contrast, *V. angustior* is a litter-dweller, staying within a few centimetres of the soil and litter (Norris and Colville 1974; Cameron et al. 2003) and does not tolerate

inundation (Cameron et al. 2003; Jankowiak and Bernard 2013; Książkiewicz 2014).

Until recently, the recognition of the species distribution over central Europe was very poor—e.g. in Poland in 2002 only four localities of *V. moulinsiana* and 20 of *V. angustior* were known. The situation has improved since 2007 and current literature reports up to 30 localities of *V. moulinsiana* and 100 localities of *V. angustior* in Poland (Książkiewicz et al. 2012; Lipińska et al. 2012). Many remaining habitats and populations (many of which may be currently unrecognised) are seriously endangered by eutrophication and natural succession resulting from abandonment of extensive usage, changes in water level, and potential infrastructure investments (e.g. Pokryszko 2003; Stebbings and Killeen 1998). It is therefore necessary to develop a strategy for effective surveys of localities of these species based on a method allowing for pinpointing areas with the highest probability of their occurrences (Guisan et al. 2006).

In this paper, we present the results of statistical modelling with the potential to increase the effectiveness of future surveys and reduce the risk of destroying small and, therefore, difficult-to-trace wetland refugia of rare vertiginid species.

Methods

Data was collected from nature conservation assessment surveys that were conducted mainly for national parks and forestry purposes. Our research was based on data from 226 localities (Fig. 1) surveyed in western, northwestern (162 localities in total), eastern (14), and southern (50) Poland during 2007–2013 (see Książkiewicz et al. 2015 for details on sampling sites).

For the surveys we selected wetlands that fitted the requirements of *V. moulinsiana* and/or *V. angustior*. We had focused on marshes covered with sedges and reed beds as well as alkaline fens located in lowland, highland, and mountainous areas (Pokryszko 1990; Killeen 2003; Cameron et al. 2003). Potential habitats were chosen based on maps, aerial photographs, and interviews with naturalists and foresters.

Because *V. angustior* and *V. moulinsiana* are rare and strictly protected by the European law we applied the least invasive method of field research. Snails were searched *in situ*, visually on vegetation and within litter and soil by one or both authors for at least 30 min, depending on the habitat area and heterogeneity. The amount of time is adequate for such surveys since experienced malacologists are generally able to detect the presence of these vertiginid species within 10 min of surveys in central European wetlands (Gołdyn and Książkiewicz in preparation).

The leaves and stems of monocots were carefully examined for *V. moulinsiana*. Litter and topsoil was sieved using a 0.5 mm sieve. Both fractions (i.e. particles passed through
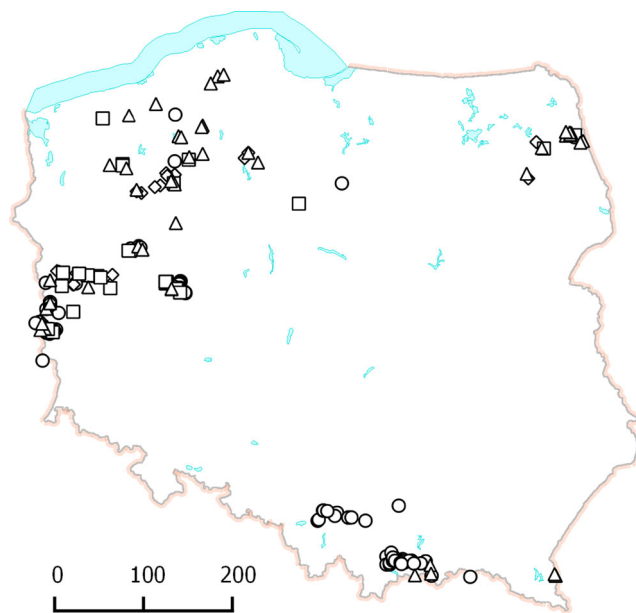
Fig. 1 Distribution of the surveyed localities over the map of Poland. *Triangles*: sites where *V. angustior* was recorded; *squares*: *V. moulinsiana*; *diamonds*: both species; *circles*: none of the species

the sieve and particles bigger than 0.5 mm in diameter) were separately examined on a white sheet of paper, using a magnifying glass.

In habitats where neither *V. angustior* nor *V. moulinsiana* were found, 2 l of the litter and topsoil were collected from ca 10 randomly chosen spots and processed in the laboratory. Each of the samples were dried and sieved using a 0.5 mm sieve. Particles passed through the sieve were examined using a stereo microscope. The > 0.5 mm fraction was checked using magnifying glass (Książkiewicz 2010).

Geomorphological landform of the terrain surrounding each locality and type of landscape were determined based on the classifications of Richling and Ostaszewska (2005; Table 1). Data regarding the general character of the locality were collected, specifying whether the surveyed plot was located in a river floodplain, lake marsh, small river valley, or temporary water body. Localisation of each plot was determined using a GPS device, and altitude was taken from topographic maps of 1:10 000 scale.

The localities were analysed for relationships between snail occurrences and geographical characteristics using Canonical Varieties Analysis (CVA) performed with CANOCO 4.5 (ter Braak and Šmilauer 2002) software. Because the species often coexist in the same locality, one model was created to test the occurrence of both species (general model) and two subsequent analyses investigated each species separately.

Geomorphological landforms and landscape types as well as altitude are not distributed evenly in Poland. The southern part of the country is covered by highlands and mountains, whereas the northern and central parts are lowland plains dominated by postglacial forms. Thus, to evaluate whether

morphology of terrain (landscape, landform, and character of the site) or its geographical location (altitude, latitude, and longitude) is more important, a variance-partitioning approach was conducted for each of the CVA models created (ter Braak 1996).

The environmental variables used in the analyses were grouped into two sets: the first was composed of site location and the second included the geomorphological data. Occurrences of vertiginid populations recorded during the surveys were included as dependent variables. Variance partitioning models were then created to separate the contributions of factors from both groups in explaining the occurrences of the studied species. Five separate CVA analyses were performed, each of them composed of data on localisation and geomorphology separately or accompanied with variables from the second group as covariables (Borcard et al. 1992). The results were compared with respect to the variance in species data explained by each model.

Variables included in the CVA models were subjected to the forward selection procedure with the Monte Carlo permutation test (5000 permutations). The overall significance of the models also was analysed with the same test. In all the statistical analyses, we considered $p=0.05$ as the minimum level when determining significance.

To make our results useful for efficient planning of future surveys, classification trees of sampled localities were created for each species. The trees show the probability of finding the given species when following one of the decision branches (nodes) with respect to the variables describing the potential site considered for a survey. Because the explanatory variables overlap partially (i.e., each site is located within one landform, one landscape type, and one descriptive category), three trees were created for each species, each of them showing classification for one such group of variables. Prior to the analysis, the dataset was randomly divided into two subsets containing equal numbers of cases. The first subset was used in the analysis as a training sample for building the model, while the other one was used for testing. The CHAID technique was used as a tree-growing method (Kass 1980). Significance values were adjusted using the Bonferroni method. Calculations were performed using SPSS 19.

Results

Vertigo moulinsiana was recorded in 71 and *V. angustior* in 88 of the 226 localities surveyed. Both species co-occurred in 41 localities.

The general CVA model showed (Fig. 2, Table 2) that with respect to the landscape forms both species occurred significantly more often in flat glaciofluvial landscapes and were not present in flooded plains. Moreover, the chances of finding *V. angustior* localities on siliceous uplands was also higher

Table 1 Types of landforms and landscapes (Richling and Ostaszewska 2005) considered in the analyses

Landform types	Abbreviation
Refashioned landforms due to glacial and glacio-fluvial deposition—in older moraine landscapes: degradational plains	degradational_plains
Landforms due to glacial and glacio-fluvial deposition in the young moraine landscapes: outwash plains	outwash_plains
Landforms due to glacial and glacio-fluvial deposition in the young moraine landscapes: morainic plateaus	morainic_plateaus
Refashioned landforms due to glacial and glacio-fluvial deposition—in older moraine landscapes: assemblages of small thaw basins and single large thaw basins	thaw_basins
Refashioned landforms due to glacial and glacio-fluvial deposition—in older moraine landscapes: relic terminal moraine ridges and hills	moraine_ridges
Horizontal and subhorizontal structures composed of Mesozoic and Neogene sedimentary rocks, affected by differentia uplift in Neogene and Quaternary times: drift-free plateaus and upland ridges of intermediate height	upland_ridges
Flysch mountains folded in the Neogene: foothills	foothills
Flysch mountains folded in the Neogene: mountains of intermediate height and low mountains de résistance, residuals	intermediate _mountains
Landforms due to fluvial accumulation: terrace flats (Pleistocene)	terrace_flats
Landforms due to fluvial accumulation: flood-plains and supra-flood plains (Holocene)	holocene_flood-plains
Landforms due to glacial and fluvio-glacial deposition in the young moraine landscapes: kames, eskers	kames_eskers
Aeolian landforms (Late Glacial and Holocene): wind-blown sandy areas	sandy_wind-blown
Landforms of biogenic origin (Holocene): peat plains	peat_plains
Landscape types	
Lowland landscapes, glacial: flat and rolling	flat_glacial
Lowland landscapes, glaciofluvial: flat and rolling	flat_glaciofluvial
Lowland landscapes, glacial: hilly	hilly_glacial
Lowland landscapes, glacial: hummocky	hummocky_glacial
Lowland landscapes, peryglacial: hummocky	hummocky_peryglacial
Lowland landscapes, eolian: hilly	hilly_eolian
Upland and low mountainous landscapes: siliceous and aluminosiliceous—erosive: forelands and low mountains	siliceous_uplands
Upland and low mountainous landscapes: carbonate and gypsum, erosive; compact massifs with klippes	carbonate_uplands
Valley and depression landscapes, overflood terraces—accumulative: terrace plains on lowlands and uplands	terrace_plains
Highland and high mountainous landscapes: highland—erosive, lower subalpine forest	accumulative_ plains
Valley and depression landscapes: marshy plains—accumulative	marshy_plains
Valley and depression landscapes: flooded valley bottoms—accumulative, flooded plains on lowlands and uplands	flooded_plains

than in the wetlands located in other landscapes. Wetlands in the landform types described as Holocene flood-plains and intermediate mountains were not favourable sites for *Vertigo* surveys, whereas those on morainic plateaus were found to be the most promising localities. Locality character and its geographical location was also important, with the following variables being significantly related to the species occurrence: marshes, floodplain, valley, longitude and latitude. The whole model explained 60.1 % of variance in species occurrences and was significant at the $p < 0.001$, $F = 15.42$ level. Variance partitioning revealed that geographical location (latitude and longitude) of the sampling plots alone explained a negligible portion of variance (3.4 %) compared to the group of other factors analysed (37.3 %) and the variance common to the two groups of variables (19.4 %).

The CVA model for *V. moulinsiana* showed that the species occurs significantly more often in flat glaciofluvial landscapes and in geomorphological landforms of morainic plateaus

(Table 3). The species is likely to be found in lake marshes and small river valleys, but floodplains and holocene flood-plain landforms are devoid of *V. moulinsiana*. Although the species was recorded more often in localities in the northern and western parts of Poland, variance partitioning showed that this relationship is of secondary importance. Localisation exclusively explained 3.5 % of variance and shared 10.7 % of explained variance with other factors. The whole model explained 48.2 % of variance in the species occurrences and was significant at the $p < 0.001$, $F = 9.60$ level.

Similarly, *V. angustior* tends to occur in sites located in small river valleys but not in floodplains (Table 4). The occurrence of the species is also connected to lake marshes; this relationship is, however, weaker compared to that of *V. moulinsiana*. *Vertigo angustior* occurred significantly less frequently in the wetlands of accumulative plains and the flooded plains landscape type and was common in wetlands of outwash plains. It was also recorded more often in localities
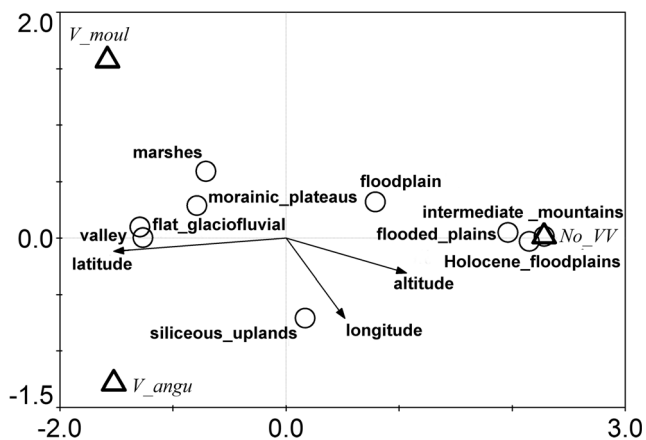
Fig. 2 CVA diagram showing the relationships between the occurrences of the two studied species (*triangles*) and the factors analysed (*circles and arrows*); No_VV =localities, where neither *V. moilinsiana* nor *V. angustior* occurred; see Table 1 for abbreviations

in the northern and western parts of Poland—again however, the significance of the geographical location was caused by the spatial distribution of other factors analysed. This group of factors exclusively explained 4.0 % of variance and shared 16.1 % with variables describing geomorphology. The whole model explained 48.2 % of variance in the species occurrences and was significant at the $p<0.001$, $F=11.46$ level.

According to the decision tree that tested *V. angustior* occurrence with respect to landform types, surveys for new localities should concentrate on areas dominated by the

Table 2 Results of the CVA analysis showing the influence of studied factors on occurrence of both, *V. moulinsiana* and *V. angustior*

Variable	LambdaA	P	F
flat_glaciofluvial	0.39	<0.001	79.51
Holocene_flood-plains	0.13	<0.001	29.91
intermediate _mountains	0.13	< 0.001	36.96
marshes	0.04	< 0.001	11.26
floodplain	0.05	< 0.001	12.89
valley	0.03	< 0.001	11.06
longitude	0.03	< 0.001	9.53
flooded_plains	0.03	< 0.001	7.73
latitude	0.02	0.001	7.57
morainic_plateaus	0.01	0.019	4.08
foothills	0.00	0.146	1.98
siliceous_uplands	0.02	0.019	4.21
altitude	0.00	0.177	1.77
terrace_flats	0.00	0.425	0.85
outwash_plains	0.01	0.762	0.27
hummocky_glacial	0.00	0.743	0.30
hummocky_peryglacial	0.00	0.633	0.44
terrace_plains	0.00	0.773	0.27

LambdaA percentage of variance explained by the variable alone; see Table 1 for abbreviations

Table 3 Results of the CVA analysis showing the influence of studied geographical factors on the occurrence of *V. moulinsiana*

Variable	LambdaA	P	F
flat_glaciofluvial	0.27	< 0.001	84.09
marshes	0.05	< 0.001	14.67
valley	0.07	< 0.001	28.24
morainic_plateaus	0.02	0.008	7.35
lat	0.02	0.035	4.56
floodplain	0.01	0.008	6.99
long	0.02	0.016	6.17
Holocene_flood-plains	0.01	0.027	5.00
alt	0.01	0.075	3.21
intermediate _mountains	0.00	0.563	0.34
outwash_plains	0.00	0.650	0.21
hummocky_peryglacial	0.00	0.503	0.44

LambdaA percentage of variance explained by the variable alone; see Table 1 for abbreviations

landforms of outwash plains (see supplementary material 1 for diagram and detailed test statistics). In such regions, the probability of finding the species in a habitat fitting its requirements reaches 74.2 % ($p<0.001$; Chi^2=20.766). If other geomorphological forms dominated the area, surveys for *V. angustior* are the most effective in Holocene flood-plains ($p<0.001$; Chi^2=18.718). The intermediate mountains should be omitted; no *V. angustior* locality actually had been found during our surveys in this landform type despite the presence

Table 4 Results of the CVA analysis showing the influence of studied geographical factors on occurrence of *V. angustior*

Variable	LambdaA	P	F
valley	0.24	< 0.001	71.37
floodplain	0.10	< 0.001	32.41
plains_accumulative	0.05	< 0.001	20.59
flooded_plains	0.04	< 0.001	15.17
longitude	0.03	0.003	9.39
marshes	0.01	0.010	6.67
latitude	0.02	0.004	8.80
outwash_plains	0.01	0.033	4.68
foothills	0.01	0.301	1.13
intermediate _mountains	0.00	0.157	1.96
altitude	0.01	0.113	2.50
siliceous_uplands	0.00	0.265	1.19
terrace_flats	0.00	0.500	0.47
holocene_flood-plains	0.00	0.279	1.17
morainic_plateaus	0.00	0.362	0.83
flat_glaciofluvial	0.01	0.564	0.34
hummocky_glacial	0.00	0.332	0.91

LambdaA percentage of variance explained by the variable alone; see Table 1 for abbreviations

of potential habitats. In regions dominated by other landforms, the probability of finding the species is 53.7 %. In the modelling of the tree, the risk estimates for training and test samples were 0.241 (SE=0.04) and 0.289 (SE=0.42), respectively.

With respect to the tree that tested the occurrence of *V. angustior* in relation to the landscape types, the results show that surveys of the species will not be effective if concentrated on flooded plains ($p<0.001$; $Chi^2=24.632$) and accumulative plains, where the probability of finding the species is very low. The surveys, however, will be more productive if focused on other landscapes where the species occurred in 62.9 % of the sites ($p<0.001$; $Chi^2=25.369$, see supplementary material 2 for a diagram and detailed test statistics).

Efficient surveys for *V. angustior* should omit margins of temporary water bodies (no such localities hosting the species were found, $p<0.001$; $Chi^2=16.95$) and concentrate on valleys of small lowland rivers ($p<0.001$; $Chi^2=19.53$). In our study, the species occurred in 69.6 % of such sites. The probability of finding *V. angustior* is further increased if examined localities are situated away from a river floodplain ($p=0.001$; $Chi^2=11.573$). In such cases, the species was found in 82.9 % of the sites; the probability of occurrence was 27.3 % otherwise. If the survey was conducted outside the small lowland valley, the probability of finding the species was 25.5 %. Searches performed within the floodplains under such conditions were ineffective ($p=0.023$; $Chi^2=5.198$), since no locality of *V. angustior* has been found in floodplains not associated with small river valleys in our surveys (Supplementary material 3).

To increase the efficiency of surveys for *V. moulinsiana*, the Holocene flood-plains ($p<0.001$; $Chi^2=18.085$) and intermediate mountains ($p<0.001$; $Chi^2=16.646$) landform types should be excluded. Focusing on other landform types will confer a 46.7 % probability of finding the species (Supplementary material 4). Also, the type of landscape surrounding the site is influential to *V. moulinsiana*; the species is more frequent in the flat glaciofluvial type (60 %) compared to other landscapes considered in our study (12 %; $p<0.001$; $Chi^2=29.047$). However, if other landscapes are to be surveyed, it is recommended that flooded plains ($p=0.006$; $Chi^2=7.434$) and accumulative plains ($p=0.011$; $Chi^2=6.523$) are omitted to increase effectiveness of the research (Supplementary material 5). The probability of finding *V. moulinsiana* is also low at the sites surrounding small, astatic waster bodies. Thus, it is justified to omit them in the surveys ($p<0.001$; $Chi^2=14.254$). The greatest effectiveness of *V. moulinsiana* surveys will be reached if they are concentrated on sites located in the valleys of small lowland rivers ($p=0.001$; $Chi^2=10.792$), where species occurrences were the most frequent within the floodplain area (88.9 % probability; $p=0.0014$; $Chi^2=6.091$). Outside the small lowland valleys, the effort should be concentrated on surveying lake marshes ($p<0.001$; $Chi^2=24.514$), where the probability of finding the species was 66.7 % (Supplementary material 6).

Discussion

Results of our study show that applying simple geographical data such as the geomorphic type of landform or landscape may increase substantially the efficiency of searching sites of *V. angustior* and *V.moulinsiana*. We show, that under the conditions of the studied area of Poland, it is possible for experienced malacologists to find these species in about 30 % of tested sites if data in the literature regarding *V. moulinsiana* and *V. angustior* habitat preferences are followed (e.g. Pokryszko 1990; Cameron et al. 2003; Killeen 2003). However, when additional data on landscape and landform types are applied, the probability of successful surveying of these species could be increased up to 83 % if undesirable locations are avoided.

The localities sampled for the present study were not distributed evenly in space, since the data resulted from nature conservation surveys performed for different purposes and their spatial distribution only partially depended on the authors. Results of variance partitioning analyses indicate however that the relationships of both species with spatial factors (longitude and latitude) are of secondary importance. The vast majority of variance explained by these factors was shared with the group of geomorphological variables. Thus, ecological factors were more important than geometric constraints (Baur et al. 2014). We therefore conclude that the uneven distribution of sampled localities does not influence the results substantially.

The major finding of our study is that the localities of *V. angustior* and *V. moulinsiana* are not distributed uniformly across wetlands in particular types of landforms and landscapes. Thus, the lack of these species does not indicate the lack of integrity of habitats located under certain geomorphological conditions. We suspect that such a situation is the result of differences in environmental conditions related to postglacial history as well as hydrogeological and climatic conditions related to this history which promoted formation of specific habitats (Price and Waddington 2000; Koralewska-Batura et al. 2010). According to our CVA analysis, both species are associated with young moraine landscapes and prefer landforms of glacial and glacio-fluvial deposition. This is consistent with data found in the current literature as both species are considered to be glacial relicts (Preece 2010). The studied vertiginids colonised areas of lowland fens, that are a succession stage of water bodies remaining after glacial retreat. Currently, such habitats still occur in the postglacial landscape, where alkaline fens and marshes are associated with lakes, as one of the final stages of lake succession (Richling and Ostaszewska 2005).

Moreover, our results suggest that *V. moulinsiana* and *V. angustior* are related to particular succession stages of lakes, with the former species occurring in more early phases of the habitat evolution. This way, *V. moulinsiana* is related to moraine plateaus dominated by the sediments of impermeable

clay. Under such conditions, the groundwater level in lake marshes is constantly high, making the habitat suitable only for the climbing vertiginid species. On the other hand, our models show that *V. angustior* occurs more often in outwash plains dominated mainly by permeable substrata such as fine sands. Lakes found in such landscapes are usually shallower due to the stronger denudation processes (Galon 1972). Thus, lakes or lake remains occurring on outwash plains represent later stages of succession dominated by non-flooded but still highly moist habitats that fit the preferences of *V. angustior.*

Our models show that both vertiginids were found significantly more often across small river valleys. In the postglacial landscapes of Central European lowlands, marshes often occur in parts of river valleys located in depressions occupied in the past by lakes. Such marshes are rich in calcium carbonates (Galon 1972) and patchy (groundwater levels and humidity are diversified).

Although *V. angustior* and *V. moulinsiana* were frequently present in the small river valleys, they were absent from floodplains and supra-floodplains shaped during Holocenic fluvial accumulation (Holocene flood-plains). Considering that old Holocene river valleys are currently related to the floodplain areas of large rivers (Galon 1972), associated habitats are often influenced by the substantial variation in the level of water and flooding events, preventing formation of habitats suitable for the land snails (e.g. Cameron et al. 2003; Plum 2005). In contrast, floodplains of small rivers are more stable: the variation of water level is lower and habitats remain moist between flooding events. Such conditions are suitable for climbing species such as *V. moulinsiana* ("floodplain" variable was not significant) however not suitable for the litter-dwellers such as *V. angustior* ("floodplain" variable was negatively related).

The "marshes" variable, referring to areas bordering lakes, was strongly related to *V. moulinsiana*. According to our study and data from the literature (Pokryszko 1990; Killeen 2003; Jueg 2004), this is one of the most typical habitats of this species. High moisture and lack of rapid changes in water level favour formation of suitable habitats for *V. moulinsiana*. Even if temporarily flooded, the species can survive by climbing up the plants (Pokryszko 1990; Hornung et al. 2003; Killeen 2003; Myzyk 2011). In case of *V. angustior*, however, survival depends on the morphology and succession stage of a lake, and, thus, habitats of lake marshes are usually too wet and do not always favour the species presence.

Both species are absent on mountainous regions probably due to the character of mountain spring fens. Such habitats, develop on shallow organo-mineral soils on slopes with significant inclination (Wołejko et al. 2008). Moreover, they are supplied by groundwater rich in calcium but poor in other nutrients (such as phosphorus and nitrogen), promoting the development of meso- and oligotrophic conditions, unfavourable for the snails studied (Sulikowska-Drozd and

Horsák 2007; Książkiewicz et al. 2012). However, according to our analyses, the potential of the presence of *V. angustior* cannot be excluded from sites located in upland and low mountain landscapes described as siliceous and aluminosiliceous erosive-forelands and low mountains (siliceous uplands). In these landscape types slopes are less inclined, and the area of fens is usually more extensive than at higher locations. The ground surface is covered with mosses, which have been shown to be a suitable habitat for *V. angustior* (Moorkens et al. 2012). Yet, compared to lowland habitats, vegetation is lower and fluctuations in groundwater levels differ, resulting in the less stable microclimate and higher amplitude of air humidity–and thus the absence of *V. moulinsiana* (Książkiewicz et al. 2013).

Following the relationships between distribution of localities of *V. moulinsiana* and *V. angustior* and geomorphology, the results of decision-tree modelling show that probability of successful surveying for these species could be increased up to 83 % when some of the locations were avoided. The predictive power could be raised when data on climate, history of usage and habitat quality are included in the models.

Even without such detailed data, our study shows that it is possible to predict the occurrence of both *Vertigo* species and avoid surveying the places where they are absent based solely on rough geomorphological data. Pinpointing habitats potentially suitable for these species is important for the following reasons: (1) the area of such places can be small and they can remain overlooked during surveys; (2) these habitats are often eutrophicated and neglected during nature conservation assessments; and (3) *Vertigo* species are very small (height of shell about 2 mm) and hard to find in the field. Thus, employing results from our study can make surveys for these vertiginids more efficient and can impact the effectiveness of their conservation (Guisan et al. 2006). By using our approach, potential conflicts between nature conservation and infrastructure development investments can be mitigated by specifying regions where the probability of the presence of *V. angustior* and *V. moulinsiana* is high (Stebbings and Killeen 1998). In this way, effective allocation of resources dedicated to surveys of the species can be performed (Marignani et al. 2014). We expect that the prediction models presented will be a useful tool in planning future surveys for *V. angustior* and *V. moulinsiana* both for the purposes of pre-investment nature conservation assessments and surveys aiming to better understand their ecology, distribution, and conservation status.

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